A replica of H.M.S. *Beagle*, the ship that carried Charles Darwin on his round-the-world journey of discovery.

Christopher Ralling

19 Development of Evolutionary Thought

Study Plan

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Why It Matters

On June 18, 1858, Charles Darwin received the shock of his life. Alfred Russel Wallace, a young naturalist working in the Asian tropics, had solicited Darwin's opinion of a short manuscript about how species change through time. Darwin quickly realized that Wallace had independently described a mechanism for biological evolution that was nearly identical to the one he had been studying for more than 20 years but had not yet described in print.

Like researchers today, scientists in the nineteenth century had to publish their work quickly to establish the "priority" on which scientific reputations are made. Darwin's friend and colleague, the geologist Charles Lyell, had encouraged him to publish a preliminary essay on evolution 2 years before Wallace's letter arrived. But Darwin procrastinated, and because Wallace was the first to prepare his work for publication, Darwin feared that history would credit the younger man with these new ideas. Despite his anxiety, Darwin forwarded Wallace's manuscript to Lyell, who passed it along to the botanist Joseph Hooker. Lyell and Hooker engineered a solution that gave credit to both men **(Figure 19.1).** On July 1, 1858, papers by Darwin and Wallace were presented to the Linnaean Society of London, a prestigious scientific organization.

Figure 19.1
Pioneers of evolutionary theory. Charles Darwin (1809–1882) and Alfred Russel Wallace (1823–1913) independently discovered the mechanism of natural selection.

Darwin worked feverishly after this harrowing experience, and his now-famous book, *On the Origin of Species by Means of Natural Selection,* was published on November 24, 1859. The first printing of 1250 copies sold out in one day. Today, we honor Darwin for developing the seminal idea about how biological evolution occurs and for the vast documentation that he accumulated over decades of study.

In *The Origin,* Darwin proposed that natural mechanisms produce and transform the diversity of life on Earth. His concept of evolution still forms the unifying intellectual paradigm within which all biological research is undertaken. Even when researchers do not address explicitly evolutionary questions, their observations, theories, hypotheses, and experiments are formulated with the implicit knowledge that all forms of life are related and have evolved from ancestral forms.

Biological evolution occurs in populations when specific *processes* cause the genomes of organisms to differ from those of their ancestors. These genetic changes, and the phenotypic modifications they cause, are the *products* of evolution. By studying the products of evolution, biologists strive to understand the processes that cause evolutionary change.

The theory of evolution is so widely accepted that most people cannot think about the biological world in any other way. But the biological changes implied by Darwin's ideas and by modern evolutionary theory had not been included in earlier worldviews.

19.1 Recognition of Evolutionary Change

The historical development of evolutionary theory is a fascinating tale of scientists struggling to reconcile evidence of change with a prevailing philosophy that change was impossible in a perfectly created universe.

Europeans Integrated Ideas from Ancient Greek Philosophy into Christian Doctrine

The Greek philosopher Aristotle (384–322 B.C.) was a keen observer of nature, and he is generally considered the first student of **natural history,** the branch of biology that examines the form and variety of organisms in their natural environments. Aristotle believed that both inanimate objects and living species had fixed characteristics. Careful study of their differences and similarities enabled him to create a ladder-like classification of nature from simplest to most complex forms: minerals ranked below plants, plants below animals, animals below humans, and humans below the gods of the spiritual realm.

By the fourteenth century, Europeans had merged Aristotle's classification with the biblical account of creation: all of the different kinds of organisms had been specially created by God, species could never change or become extinct, and new species could never arise. Biological research became dominated by **natural theology,** which sought to name and catalog all of God's creation. Careful study of each species would identify its position and purpose in the *Scala Naturae,* or Great Chain of Being, as Aristotle's ladder of life was called. In the eighteenth century, the Swedish botanist Carolus Linnaeus (1707–1778), who developed the science of **taxonomy,** the branch of biology that classifies organisms (see Chapter 23), undertook this important work *ad majorem Dei gloriam* ("for the greater glory of God").

Scholars also used a literal interpretation of scripture to date the time of creation precisely. By tabulating the human generations described in the Bible, they determined that the creation had occurred around 4000 B.C., making Earth a bit less than 6000 years old. Thus, Earth hardly seemed old enough for much change to have taken place.

Scientists Slowly Became Aware of Change in the Natural World

Modern science came of age in the fifteenth through eighteenth centuries. The English philosopher and statesman Sir Francis Bacon (1561–1626) established the importance of observation, experimentation, and inductive reasoning. Other scientists, notably Nicolaus Copernicus (1473–1543), Galileo Galilei (1564–1642), René Descartes (1596–1650), and Sir Isaac Newton (1643–1727), proposed mechanistic theories to explain physical events. In addition, three new disciplines—biogeography, comparative morphology, and geology—promoted a growing awareness of change.

Questions about Biogeography. As long as naturalists encountered organisms only from Europe and surrounding lands, the task of understanding the *Scala Naturae* was manageable. But global explorations in the fifteenth through seventeenth centuries provided

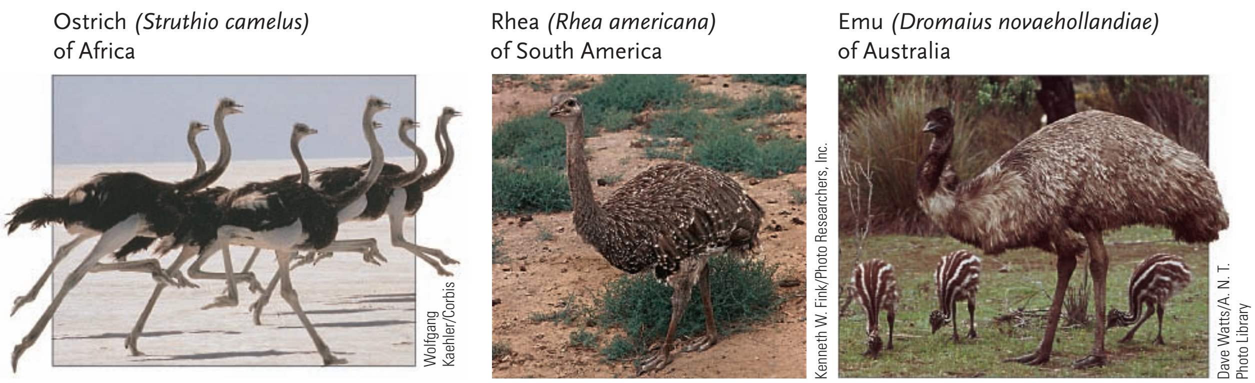


Figure 19.2
Large, flightless birds. Three large bird species with greatly reduced wings occupy similar habitats in geographically separated regions.

naturalists with thousands of unknown plants and animals from Asia, sub-Saharan Africa, the Pacific Islands, and the Americas. Although some were similar to European species, others were new and very strange.

Studies of the world distribution of plants and animals, now called **biogeography**, raised puzzling questions. Was there no limit to the number of species created by God? Where did all these species fit in the *Scala Naturae*? If all species had been created in the Garden of Eden, why were the species found in Africa or Asia different from those found in Europe? Why was each species found only in certain places and not others **(Figure 19.2)?**

Questions about Comparative Morphology. When biologists began to compare the **morphology** (anatomical structure) of organisms, they discovered interesting similarities and differences. For example, the front legs of pigs, the flippers of dolphins, and the wings of bats differ markedly in size, shape, and function **(Figure 19.3).** But these appendages have similar locations in the animals' bodies; all are constructed of bones, muscles, and skin; and all develop similarly in the animals' embryos. If these limbs were specially created for different means of locomotion, why didn't the Creator use different materials and structures for walking, swimming, and flying?

Natural theologians answered that some general body plans were perfect, and there was no need to invent a new plan for every species. But a French scientist, George-Louis Leclerc (1707–1788), le Comte (Count) de Buffon, was still puzzled by the existence of body parts with no apparent function. For example, he noted that the feet of pigs and some other mammals have two toes that never touch the ground (see Figure 19.3). If each species is anatomically perfect for its particular way of life, why do useless structures exist?

Buffon proposed that some animals must have *changed* since their creation; he suggested that **vestigial structures**, the useless parts we observe today, must have functioned in ancestral organisms. Buffon offered no explanation of how functional structures became vestigial, but he clearly recognized that some species were "conceived by Nature and produced by Time."

Questions about Fossils. By the mid-eighteenth century, geologists were mapping the **stratification**, or horizontal layering, of sedimentary rocks beneath the soil surface (see Figure 22.3). Different layers held different kinds of **fossils** (*fossilis* = dug up). Relatively small and simple fossils appeared in the deepest layers. Fossils in the layers above them were more complex. Those in the uppermost layers often resembled living organisms. Moreover, fossils found in any particular layer were often similar, even if they were collected from geographically separated sites. What were these fossils, and why did they vary more from one layer of

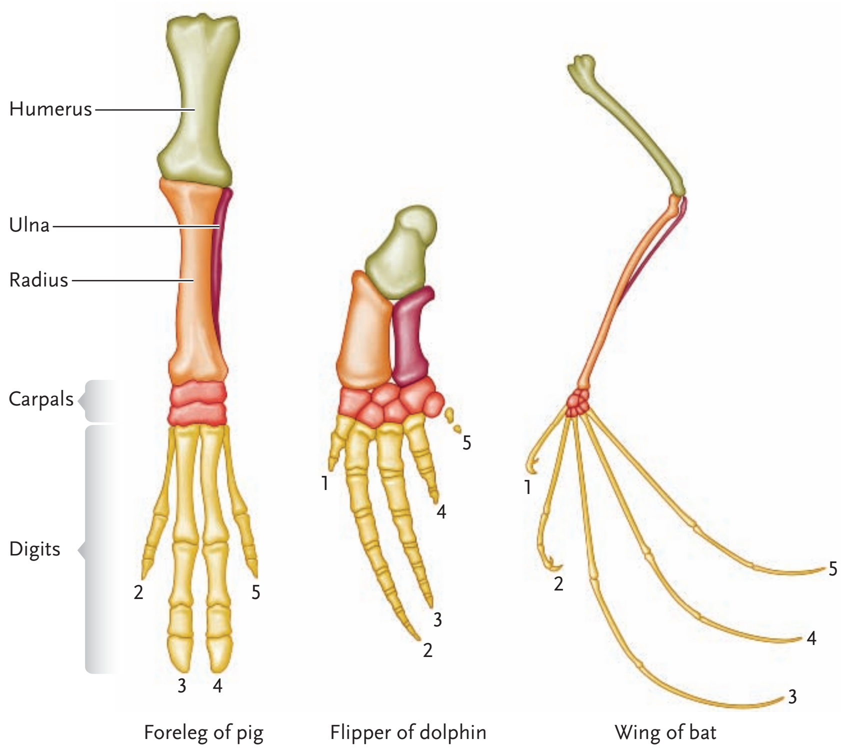


Figure 19.3
Mammalian forelimbs and locomotion. Pigs use their legs to walk or run, dolphins use their flippers to swim, and bats use their wings to fly. Homologous bones are pictured in the same color, and digits (fingers) are numbered; pigs have lost the first digit over evolutionary time.

rock to another than from one geographical region to another?

Some scientists suggested that fossils were the remains of extinct organisms, but natural theology did not allow extinction. Thomas Jefferson, the third president of the United States and an amateur fossil hunter, thought that fossils were the remains of species that were now extremely rare; he believed that nature could not have "permitted any one race of her animals to become extinct" or "formed any link in her great works so weak [as] to be broken." He even asked Lewis and Clark to keep an eye out for giant ground sloths, now known to be extinct, during their exploration of the Pacific Northwest.

Georges Cuvier (1769–1832), a French zoologist and a founder of comparative morphology, as well as **paleobiology** (the study of ancient organisms), realized that the layers of fossils represented organisms that had lived at successive times in the past. He suggested that the abrupt changes between geological strata marked dramatic shifts in ancient environments. Cuvier and his followers developed the theory of **catastrophism**, reasoning that each layer of fossils represented the remains of organisms that had died in a local catastrophe, such as a flood. Somewhat different species then recolonized the area, and when another catastrophe struck, they formed a different set of fossils in the next higher layer.

Lamarck Developed an Early Theory of Biological Evolution

A contemporary of Cuvier and a student of Buffon, Jean Baptiste de Lamarck (1744–1829) proposed the first comprehensive theory of biological evolution based on specific mechanisms. He proposed that a metaphysical "perfecting principle" caused organisms to become better suited to their environments. Simple organisms evolved into more complex ones, moving up the ladder of life; microscopic organisms were replaced at the bottom by spontaneous generation.

Lamarck theorized that two mechanisms fostered evolutionary change. According to his *principle of use and disuse,* body parts grow in proportion to how much they are used, as anyone who "pumps iron" well knows. Conversely, structures that are not often used get weaker and shrink, such as the muscles of an arm immobilized in a cast. According to his second principle, the *inheritance of acquired characteristics,* changes that an animal acquires during its lifetime are inherited by its offspring. Thus, Lamarck argued that long-legged wading birds, such as herons **(Figure 19.4),** are descended from short-legged ancestors that stretched their legs to stay dry while feeding in shallow water. Their offspring inherited slightly longer legs, and after many generations, their legs became extremely long.


Rich Kirchner/Foto Natura/Photo Researchers, Inc.

Figure 19.4
A great blue heron *(Ardea herodias)*. Like many other wading birds, herons have long, stiltlike legs.

Today, we know that Lamarck's proposed mechanisms do not cause evolutionary change. Although muscles do grow larger through continued use, most structures do not respond in the way Lamarck predicted. Moreover, structural changes acquired during an organism's lifetime are not inherited by the next generation. Even in his own day, Lamarck's ideas were not widely accepted.

Despite the shortcomings of his theory, Lamarck made four tremendously important contributions to the development of an evolutionary worldview. First, he proposed that all species change through time. Second, he recognized that new characteristics are passed from one generation to the next. Third, he suggested that organisms change in response to their environments. And fourth, he hypothesized the existence of specific mechanisms that caused evolutionary change. The first three of these ideas became cornerstones of Darwin's evolutionary theory. Perhaps Lamarck's most important contribution was that he fostered discussion. By the mid-nineteenth century, most educated Europeans were talking about evolutionary change, whether they believed in it or not.

Geologists Recognized That Earth Had Changed over Time

In 1795, the Scottish geologist James Hutton (1726–1797) argued that slow and continuous physical processes, *acting over long periods of time,* produced Earth's major geological features; for example, the movement of water in a river slowly erodes the land and deposits sediments near the mouth of the river. Given enough time, erosion creates deep canyons, and sedimentation creates thick topsoil on flood plains. Hutton's **gradualism,** the view that Earth changed *slowly* over its history, contrasted sharply with Cuvier's catastrophism.

The English geologist Charles Lyell (1797–1875) championed and extended Hutton's ideas in an influential series of books, *Principles of Geology.* Lyell argued that the geological processes that sculpted Earth's surface over long periods of time—such as volcanic eruptions, earthquakes, erosion, and the formation and movement of glaciers—are exactly the same as the processes observed today. This concept, **uniformitarianism,** undermined any remaining notions of an unchanging Earth. Also, because geological processes proceed very slowly, it must have taken millions of years, not just a few thousand, to mold the landscape into its current configuration.

Study Break

1. Why did the existence of vestigial structures make Buffon question the idea that living systems never changed?
2. What were Lamarck's contributions to an evolutionary worldview?
3. How do the concepts of gradualism and uniformitarianism in geology undermine the belief that Earth is only about 6000 years old?

Figure 19.5
Darwin's voyage. H.M.S. *Beagle* circumnavigated the globe between 1831 and 1836.

19.2 Darwin's Journeys

In 1831, in the midst of this intellectual ferment, young Charles Darwin wondered what to do with his life. Raised in a wealthy English household, he had always collected shells and studied the habits of insects and birds; he preferred hunting and fishing to classical studies. Despite lackluster performance as a student, Darwin was expected to continue the family tradition of practicing medicine. But he abandoned medical studies after 2 years. Instead, he followed his interest in natural history over the objections of his father, who reputedly told him, "You care for nothing but shooting, dogs, and rat-catching and you will be a disgrace to yourself and all of your family."

At the suggestion of his father, Darwin studied for a career as a clergyman, earning a degree at Cambridge University. There, he found a mentor in the Reverend John Henslow, a leading botanist, who arranged for Darwin to travel as the captain's dining companion aboard H.M.S. *Beagle,* a naval surveying ship. Darwin thus embarked on a sea voyage and an intellectual journey that altered the foundations of modern thought.

Darwin Saw the World on the Voyage of the *Beagle*

The *Beagle* sailed westward to map the coastline of South America and then circumnavigated the globe **(Figure 19.5).** When the ship's naturalist quit his post midjourney, Darwin replaced him in an unofficial capacity. For nearly 5 years Darwin toured the world, and because he suffered from seasickness, he seized every chance to go ashore. He collected plants and animals in Brazilian rain forests and fossils in Patagonia. He hiked the grasslands of the pampas and climbed the Andes in Chile. Armed with Henslow's parting gift, the first volume of Lyell's *Principles of Geology,* Darwin was primed to apply gradualism and uniformitarianism to the living world.

What Darwin Saw. When he began his travels, Darwin had no clue that biological evolution had produced the mind-boggling variety of species that he would encounter. Three broad sets of observations later helped him unravel the mystery of evolutionary change.

First, while exploring along the coast of Argentina, Darwin discovered fossils that often resembled organisms that inhabit the same region today. For example, despite an enormous size difference, living armadillos and fossilized glyptodonts had similar body armor, but they were unlike any other species known to science **(Figure 19.6).** If both species had been created at the same time and both were found in South America, why didn't glyptodonts live alongside armadillos? Darwin later wondered whether armadillos might be the living descendants of the now-extinct glyptodonts.

Second, Darwin observed that the animals he encountered in different South American habitats clearly resembled each other but differed from species that occupied similar habitats in Europe. For example, he

Charles R. Knight painting (negative CK21T), Field Museum of Natural History, Chicago

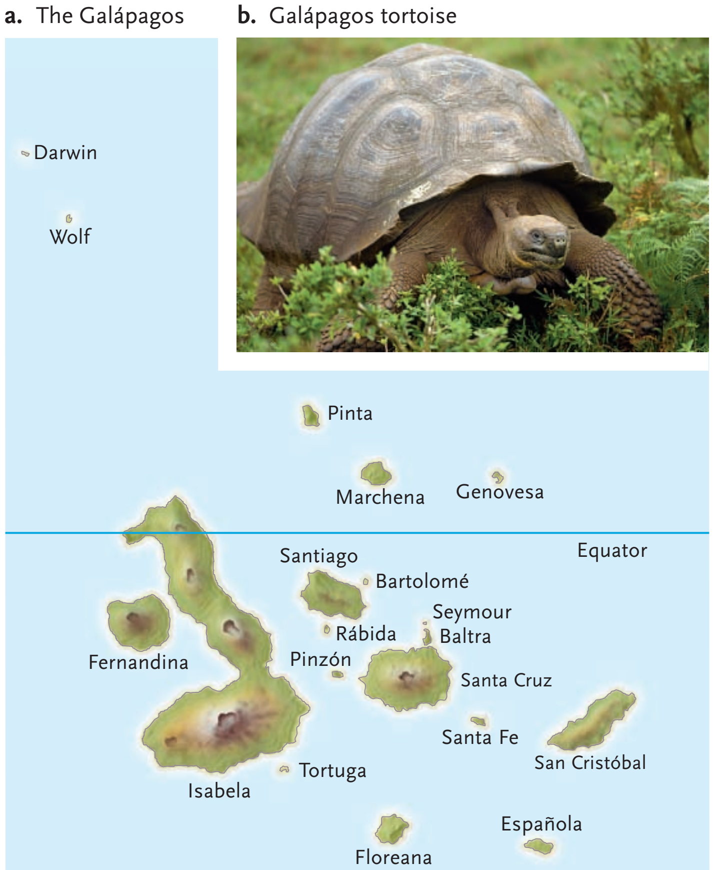
Calvin Larsen/Photo Researchers, Inc.

Figure 19.6
Ancestors and descendants. An extinct glyptodont (top) probably weighed 300 to 400 times as much as its living descendant, a nine-banded armadillo *(Dasypus novemcinctus).*

a. South American nutria **b.** European beaver

Figure 19.7
Morphologic differences in species from different continents. Darwin noted that **(a)** South American nutria *(Myocastor coypus)* and **(b)** European beavers *(Castor fiber)* differ in appearance, even though both species are aquatic rodents that feed on vegetation. Notice that nutria have long, round tails, whereas beavers have short, flat tails.

a. The Galápagos **b.** Galápagos tortoise **c.** Marine iguana



d. Blue-footed booby

Figure 19.8
The Galápagos. (a) Volcanic eruptions created the Galápagos archipelago (located 1000 km west of Ecuador) between 3 and 5 million years ago. **(b)** The islands were named for the giant tortoises found there (in Spanish, *galápa* means tortoise); this tortoise *(Geochelone elephantopus)* is native to Isla Santa Cruz. **(c)** Marine iguanas *(Amblyrhynchus cristatus)* dive into the Pacific Ocean to feed on algae. **(d)** A male blue-footed booby *(Sula nebouxii)* engages in a courtship display.

a. *Certhidea olivacea* **b.** *Geospiza scandens* **c.** *Geospiza magnirostris* **d.** *Camarhynchus pallidus*

Figure 19.9
Bill shape and food habits. The 13 finch species that inhabit the Galápagos are descended from a common ancestor, a seed-eating ground finch that migrated to the islands from South America. **(a)** *Certhidea olivacea* uses its slender bill to probe for insects in vegetation. **(b)** *Geospiza scandens* has a medium-sized bill suitable for eating cactus flowers and fruit. **(c)** *Geospiza magnirostris* uses its thick, strong bill to crush cactus seeds. **(d)** *Camarhynchus pallidus* uses its bill to hammer at bark and to hold cactus spines, with which it probes for wood-boring insects, such as termites.

noted that nutria *(Myocastor coypus)*, a semiaquatic rodent in South America, bore a closer resemblance to rodent species from the mountains or grasslands of that continent than it did to the European beaver *(Castor fiber)*, another semiaquatic rodent that had once been common in England **(Figure 19.7)**. Why did animals from markedly different South American environments resemble each other, and why were animals that lived in similar environments on separate continents different? Darwin later understood that animals in South America resembled each other because they had inherited their similarities from a common ancestor.

Third, Darwin observed fascinating patterns in the distributions of species on the Galápagos **(Figure 19.8)**. There he found strange and wonderful creatures, including giant tortoises and lizards that dove into the sea to feed on algae. Darwin quickly noted that the animals on different islands varied slightly in form. Indeed, experienced sailors could easily identify a tortoise's island of origin by the shape of its shell. Moreover, many species resembled those on the distant South American mainland. Why did so many different organisms occupy one small island cluster, and why did these species resemble others from the nearest continent? Darwin later hypothesized that the plants and animals of the Galápagos were descended from South American ancestors, and that each species had changed after being isolated on a particular island.

Darwin's Reflections after His Voyage. The *Beagle* returned to England in 1836, and Darwin began his first notebook on the *Transmutation of Species* the following year. He realized that changes in species over time provided the only plausible explanation for his observations.

A diverse group of finches from the Galápagos **(Figure 19.9)** provided the single greatest spark for Darwin's work. He had noticed great variability in the shapes of their bills, but he had incorrectly assumed that birds on different islands belonged to the same species. Thus, he had not recorded the island where he had captured each specimen. Luckily, the *Beagle*'s captain, Robert Fitzroy, had more thoroughly documented his own collection, allowing Darwin to study the relationships and geographical distributions of a dozen species. As Darwin reviewed his data, he began to focus on two aspects of a general problem. Why were the finches on a particular island slightly different from those on nearby islands, and how did all these different species arise?

Darwin Used Common Knowledge and Several Inferences to Develop His Theory

With a substantial inheritance and burdened by chronic illness, Darwin led a reclusive life as he embarked on an intellectual journey every bit as exciting as his voyage on the *Beagle* (see *Focus on Research*). His lifetime goal was to accumulate evidence of evolutionary change and identify the mechanism that caused it.

Selective Breeding and Heredity. Having grown up in the country, Darwin was well aware that "like begets like"; that is, offspring frequently resemble their parents. Plant and animal breeders had applied this basic truth of inheritance for thousands of years. By

Focus on Research

Basic Research: Charles Darwin's Life as a Scientist

Darwin's observations during the voyage of H.M.S. *Beagle* convinced him that species change through time, and that natural processes produced Earth's biodiversity. He spent the rest of his life gathering data to support his ideas and unravel the workings of natural selection.

Shortly after the *Beagle* returned to England in 1836, Darwin began his first notebook on the "transmutation of species." But he put his study of evolution aside while he wrote up the geological and biological research that he had undertaken during the voyage. This task took him 10 years to complete—twice as long as the journey itself. The results of these efforts were numerous articles and several books, including the now famous *Journal of the Voyage of the Beagle,* published in 1839.

After preparing a sketch of his ideas about evolution in 1844, Darwin continued to write up his observations from the voyage. But he had trouble classifying one species of barnacle, a small marine invertebrate, which he had collected in Chile. For the next 8 years he studied barnacles, examining more than 10,000 specimens and revising the entire classification of these animals. His colleagues saw this study as a strange diversion from his work on evolution, but Darwin's detailed examination of barnacle anatomy sharpened his observational skills and provided a test case in which he could apply his ideas about descent with modification to a large and diverse group of organisms. He published four volumes about barnacles in 1854.

While studying barnacles, Darwin continued to think about "the species question." He kept notebooks about variation in plants and animals, focusing on variation that was amplified by selective breeding. He was a tireless collector of facts, which he sought from every possible source. He badgered dog breeders, horse farmers, and horticulturists with long lists of questions about their work. His enthusiasm was infectious, and workers throughout the world supplied him with data and specimens. Darwin was also an eager and skilled experimentalist, and he took up pigeon breeding, marveling at the huge variety of morphological traits that he and other breeders could produce. In the late 1850s, a communication from another naturalist, Alfred Russel Wallace, forced him to finally complete *The Origin,* which revolutionized the study of biology.

Even after *The Origin* was published, Darwin continued to gather facts and write about evolution, working almost up to the day he died in 1882 at age 74. He published a detailed analysis of how earthworms improve the soil *(The Formation of Vegetable Mould through the Action of Worms)* and wrote books on several botanical topics, among them plants that eat animals *(Insectivorous Plants),* pollination and fertilization systems *(Fertilisation in Orchids* and *The Effects of Self- and Cross-Fertilisation),* and the tendency of plants to grow toward sunlight *(The Power of Movement in Plants)*. Darwin's work always had an evolutionary focus, however, and he produced several revisions of *The Origin,* as well as books on artificial selection *(Variation of Animals and Plants under Domestication),* human ancestry *(The Descent of Man),* and animal behavior *(The Expression of the Emotions in Men and Animals)*.

William Perlman/Star Ledger/Corbis

Darwin's study. Darwin undertook most of his life's work in this room at Down House. He hesitated to discard old papers and specimens, believing that he would find a use for them as soon as they were carried away in the trash.

selectively breeding individuals with favorable characteristics, they enhanced those traits in future generations.

Farmers use selective breeding to improve domesticated plants and animals. If one cow produces more milk than any other, the farmer selectively breeds her (rather than others), hoping that her offspring will also be good milk producers. Although the mechanism of heredity was not yet understood, this principle had been applied countless times to produce bigger beets, plumper pigs, and fancier pigeons (see Figure 1.10). Darwin was well aware of this process, which he called **artificial selection**, but he puzzled over how it could operate in nature. (*Insights from the Molecular Revolu-*

Insights from the Molecular Revolution

Artificial Selection in the Test Tube

From Darwin's time until very recently, artificial selection was the province of plant and animal breeders, who chose individuals with desired traits to be the parents of the next generation. Now the laborious and time-consuming techniques of the breeders have been bypassed by rapid artificial selection experiments on DNA and protein molecules in the test tube.

One example of artificial selection in the test tube was provided by John J. Toole and his colleagues at Gilead Sciences in Foster City, California. They were interested in developing DNA molecules that could interfere with blood clotting by binding to thrombin, a blood protein that forms a major part of blood clots. The DNA could be used to treat people who are in danger of developing blood clots that might clog arteries in the heart, brain, or other critical organs. Nucleic acid molecules would be particularly useful as anticlotting agents because, unlike the proteins now used for this purpose, they rarely induce an immune reaction in the person being treated.

The investigators began their experiments by using a commercially available apparatus to make short, artificial DNA molecules of random sequence. They ran the apparatus long enough to produce more than 10^{13} (10 trillion!) different DNA sequences, and then made multiple copies of the sequences using the polymerase chain reaction (PCR; see Section 18.1). To select for DNA molecules that could bind to thrombin, they poured the entire DNA preparation through a column that contained thrombin molecules attached to glass beads. Only a few sequences among the trillions, about 0.01% of the total DNA sample, were able to bind strongly to thrombin. The researchers used PCR to multiply the sequences they had captured, generating 10 trillion "progeny" molecules. These progeny DNA molecules were poured through another column that contained thrombin molecules attached to glass beads. This time, a larger percentage of the molecules bound strongly to the thrombin molecules. These strongly binding DNA molecules were then used as the "parents" to generate another 10 trillion progeny. After five repetitions of the total process, producing five generations of DNA molecules, 40% of the DNA molecules in the preparation could recognize and bind strongly to thrombin.

The final products of the artificial selection were tested for their ability to interfere with the activity of thrombin in the blood clotting reaction. These experiments were successful; the antithrombin DNA molecules are being tested in monkeys and baboons, in which they appear to work effectively as anticlotting agents.

Toole and his team thus mimicked the evolutionary process on the molecular scale. Their experimental process selected DNA molecules that could bind to thrombin from the many random nucleotide sequences available in the test tube. The sequences that survived the selection test produced the greatest number of progeny molecules in the next generation. The same selection pressure, exerted over five generations of progeny molecules, greatly increased the percentage that could bind strongly to the protein. As a result, the DNA population evolved in the test tube from one with little or no ability to bind thrombin to one with high ability.

This approach is being used in many laboratories to develop DNA and RNA molecules with desired functions. By starting with DNA molecules that encode enzymes, researchers hope to select biological catalysts that can speed chemical reactions with scientific, medical, or industrial purposes.

tion describes how modern researchers apply artificial selection to molecules in a test tube.)

The Struggle for Existence. Darwin had a revelation about how selective breeding could occur naturally when he read the famous publication by Thomas Malthus, *Essay on the Principles of Population*. Malthus, an English clergyman and economist, was worried about the fate of the nation's poor. England's population was growing much faster than its agricultural capacity, and with individuals competing for limited food resources, some would inevitably starve.

Darwin applied Malthus's argument to organisms in nature. Species typically produce many more offspring than are needed to replace the parent generation, yet the world is not overrun with sunflowers, tortoises, or bears. Darwin even calculated that, if its reproduction went unchecked, a single pair of elephants, the slowest breeding animal known, would leave roughly 19 million descendants after only 750 years. Happily for us (and all other species that might get underfoot), the world is not so crowded with elephants. Instead, some members of every population survive and reproduce, whereas others die without reproducing.

Darwin's Inferences. Darwin's discovery of a mechanism for evolutionary change required him to infer the nature of a process that no one had envisioned, much less documented **(Table 19.1).** First, individuals within populations vary in size, form, color, behavior, and other characteristics. Second, many of these variations are hereditary. What if variations in hereditary traits enabled some individuals to survive and reproduce more than others? Organisms with favorable traits would leave many offspring, whereas those that lacked favorable traits would die leaving

Table 19.1 **Darwin's Observations and Inferences about Evolution by Means of Natural Selection**

Observations	Inferences	
Most organisms produce more than one or two offspring.	Individuals within a population compete for limited resources.	A population's characteristics will change over the generations as advantageous, heritable characteristics become more common.
Populations do not increase in size indefinitely.		
Food and other resources are limited for most populations.		
Individuals within populations exhibit variability in many characteristics.	Hereditary characteristics may allow some individuals to survive longer and reproduce more than others.	
Many variations have a genetic basis that is inherited by subsequent generations.		

few, if any, descendants. Thus, favorable hereditary traits would become more common in the next generation. If the next generation was subjected to the same process of selection, the traits would be even more common in the third generation. Because this process is analogous to artificial selection, Darwin called it **natural selection.**

As an evolutionary mechanism, natural selection favors **adaptive traits,** genetically based characteristics that make organisms more likely to survive and reproduce. And by favoring individuals that are well adapted to the environments in which they live, natural selection causes species to change through time. As shown in Figure 19.9, each species of Galápagos finch has a distinctive bill. Variations in bill size and shape make some birds better adapted for crushing seeds and others for capturing insects. Imagine an island where large seeds were the only food available; individuals with a stout bill would be more likely to survive and reproduce than would birds with slender bills. These favored individuals would pass the genes that produce stout bills to their descendants, and after many generations, their bills might resemble those of *Geospiza magnirostris* (see Figure 19.9c). Natural selection also changes nonmorphologic characteristics of populations; for example, insect populations that are exposed to insecticides develop resistance to these toxic chemicals over time (see Figure 19.11).

Darwin realized that natural selection could also account for striking differences between populations and, given enough time, for the production of new species. For example, suppose that small insects were the only food available to finches on a different island. Birds with long thin bills might be favored by natural selection, and the population of finches might eventually possess a bill shaped like that of *Certhidea olivacea* (see Figure 19.9a). If we apply parallel reasoning to the many characteristics that affect survival and reproduction, natural selection would cause the populations to become more different over time, a process called **evolutionary divergence.**

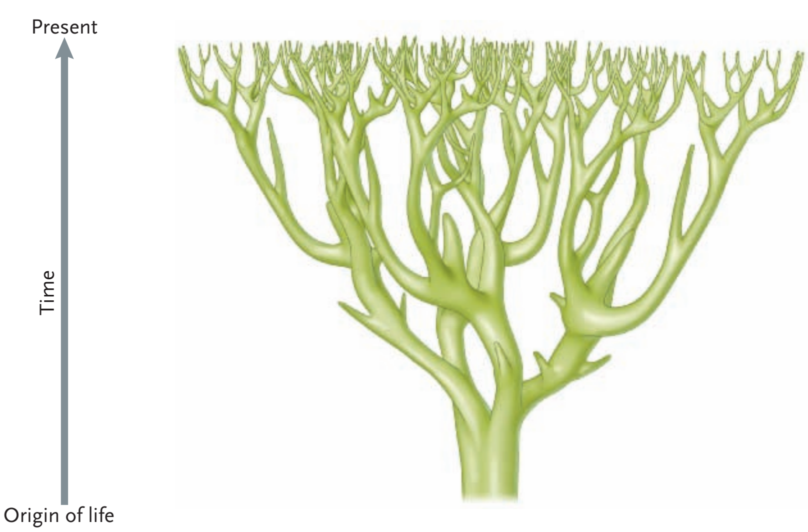


Figure 19.10
The tree of life. Darwin envisioned the history of life as a tree. Branching points represent the origins of new lineages; branches that do not reach the top represent extinct groups.

Darwin's Theory Revolutionized the Way We Think about the Living World

It would be hard to overestimate the impact of Darwin's theory on Western thought. In *The Origin,* Darwin proposed a logical mechanism for evolutionary change and provided enough supporting evidence to convince the educated public.

Darwin argued that all the organisms that have ever lived arose through **descent with modification,** the evolutionary alteration and diversification of ancestral species. He envisioned this pattern of descent as a tree growing through time **(Figure 19.10).** The base of the trunk represents the ancestor of all organisms. Branching points above it represent the evolutionary divergence of ancestors into their descendants. Each limb represents a body plan suitable for a particular way of life; smaller branches represent more narrowly defined groups of organisms; and the uppermost twigs represent living species.

Darwin proposed natural selection as the mechanism that drives evolutionary change. In fact, most of *The Origin* was an explanation of how natural selection acted on the variability within groups of organisms, preserving favorable traits and eliminating unfavorable ones.

Four characteristics distinguish Darwin's theory from earlier explanations of biological diversity and adaptive traits:

1. Darwin provided purely physical, rather than spiritual, explanations about the origins of biological diversity.
2. Darwin recognized that evolutionary change occurs in groups of organisms, rather than in individuals: some members of a group survive and reproduce more successfully than others.
3. Darwin described evolution as a multistage process: variations arise within groups, natural selection eliminates unsuccessful variations, and the next generation inherits successful variations.
4. Like Lamarck, Darwin understood that evolution occurs because some organisms function better than others *in a particular environment*.

What is most amazing about Darwin's intellectual achievement is that he knew nothing about Mendelian genetics (see Chapter 12). Thus, he had no clear idea of how variation arose or how it was passed from one generation to the next.

Evolution was a popular topic in Victorian England, and Darwin's theory was both praised and ridiculed. Although he had not speculated about the evolution of humans in *The Origin*, many readers were quick to extrapolate Darwin's ideas to our own species. Needless to say, certain influential Victorians were not amused by the suggestion that humans and apes share a common ancestry.

Nevertheless, Darwin's painstaking logic and careful documentation convinced most readers that evolution really does take place. Thomas Huxley, so staunch an advocate that he was known as "Darwin's bulldog," summed up the reaction of many when he quipped that the theory was so obvious, once articulated, that he was surprised he had not thought of it himself. Darwin's vision of common ancestry quickly became the intellectual framework for nearly all biological research. Many readers, however, did not readily accept the mechanism of natural selection. The major stumbling block was that Darwin had not provided any plausible theory of heredity.

Study Break

1. What observations that Darwin made on his round-the-world voyage influenced his later thoughts about evolution?
2. How did Darwin's understanding of artificial selection enable him to envision the process of natural selection?
3. What were the four great intellectual triumphs of Darwin's theory?

19.3 Evolutionary Biology since Darwin

Although Gregor Mendel published his work on genetics in 1866, it was not well known in England until 1900. At that time, scientists perceived a fundamental conflict between Darwin's and Mendel's theories. One problem was that Darwin had used complex characteristics, such as the structure of bird bills, to illustrate how natural selection worked. We now know that at least several genes often control such traits. By contrast, Mendel had studied simpler characteristics, such as the height of pea plants (see Chapter 12). A single gene often controls simple traits, which is one reason Mendel could interpret his experimental results so clearly. Biologists had a hard time applying Mendel's straightforward experimental results to Darwin's complex examples.

A second problem arose because Darwin believed that biological evolution occurred gradually over many generations. However, early twentieth-century geneticists, focusing on simple traits such as those Mendel had studied, sometimes observed very rapid and dramatic changes in certain characteristics. A widely accepted theory, *mutationism* suggested that evolution occurred in spurts, induced by the chance appearance of "hopeful monsters," rather than by gradual change.

The Modern Synthesis Created a Unified Theory of Evolution

In the 1910s and 1920s, geneticists and mathematicians forged a critical link between Darwinism and Mendelism. The new discipline, **population genetics**, recognized the importance of genetic variation as the raw material of evolution. Population geneticists constructed mathematical models, which applied equally well to simple and complex traits, to predict how natural selection and other processes influence a population's genetics.

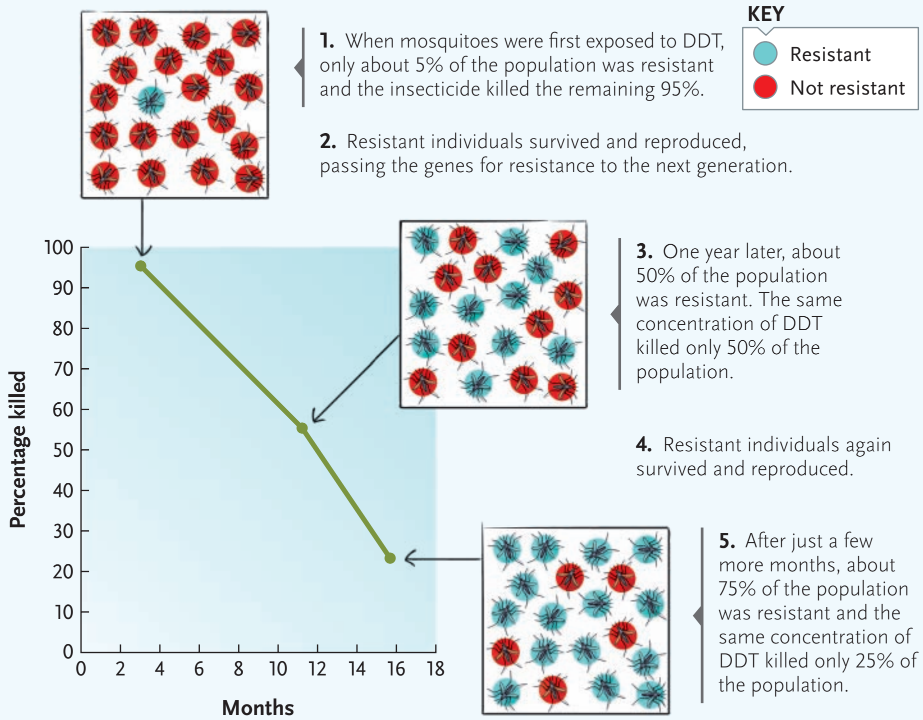
In the 1930s and 1940s, a unified theory of evolution, the **modern synthesis**, interpreted data from biogeography, comparative morphology, comparative

Figure 19.11 Experimental Research

How Exposure to Insecticide Fosters the Evolution of Insecticide Resistance

QUESTION: Does exposure to insecticide foster the evolution of insecticide resistance in insect populations?

EXPERIMENT: Researchers studied samples of wild mosquitoes *(Anopheles culicifacies)* captured at a small village in India, where public health officials frequently sprayed the insecticide dichloro-diphenyl-trichloroethane (DDT) to control these pests. For each test, the researchers exposed samples of mosquitoes to a 4% concentration of DDT for 1 hour and then measured the percentage that died during the next 24 hours. Tests were repeated 12 months and 16 months after the first experiment.



RESULTS: Over the course of the experiment, smaller and smaller percentages of the mosquitoes died after their exposure to the test concentration of the insecticide.

CONCLUSION: The indiscriminate use of DDT established natural selection that favored DDT-resistant individuals. Exposure to DDT therefore fostered the evolution of an adaptive resistance to DDT in the mosquito population.

embryology, paleontology, and taxonomy within an evolutionary framework. The authors of the modern synthesis focused on evolutionary change within populations, and although they considered natural selection the primary mechanism of evolution, they acknowledged the importance of other processes (see Chapter 20). Proponents of the modern synthesis also embraced Darwin's idea of gradualism and deemphasized the significance of mutations that changed traits suddenly and dramatically.

The modern synthesis also tried to link the two levels of evolutionary change that Darwin had identified: microevolution and macroevolution. **Microevolution** describes the small-scale genetic changes that populations undergo, often in response to shifting environmental circumstances; a small evolutionary shift in the size of the bill of a finch species is an example of microevolution. **Macroevolution** describes large-scale patterns in the history of life, such as the appearance and then relatively sudden disappearance of gigantic dinosaurs. According to the modern synthesis, macroevolution results from the gradual accumulation of microevolutionary changes, but researchers are just beginning to unravel the genetic mechanisms that establish a relationship between these two levels of evolutionary change (see Chapter 22).

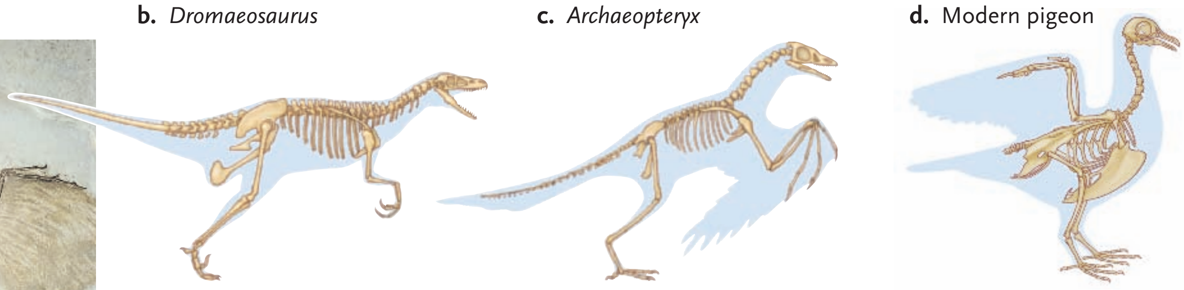


Figure 19.12
Bird ancestry. **(a)** One of the few known fossils of *Archaeopteryx lithographica*, from limestone deposits more than 140 million years old. **(b)** *Dromaeosaurus* was a small, bipedal dinosaur that had teeth, long limbs with toes and fingers, and a long, bony tail. **(c)** *Archaeopteryx* shared those three traits with *Dromaeosaurus*, but it also had feathers and hollow bones, characteristics that it shares with modern birds. **(d)** Modern birds, such as the pigeon, have long limbs similar to those of *Dromaeosaurus* and *Archaeopteryx*, but their fingers and bony tails are greatly reduced; like *Archaeopteryx*, their bodies are covered with feathers, but a horny bill has replaced their teeth.

Research in Many Fields Has Provided Evidence of Evolutionary Change

During the past 100 years, scientists have assembled a huge and compelling body of evidence from many biological disciplines indicating that biological evolution is a fact of life on Earth.

Adaptation by Natural Selection. Biologists interpret the products of natural selection as evolutionary adaptations. For example, the wings of birds, which have been modified by evolutionary processes over millions of years, have an obvious function that helps these animals survive and reproduce. Sometimes, however, natural selection operates on a short time scale, as illustrated by the development of pesticide resistance in insects. When we first use a new pesticide, a low concentration often kills a large percentage of the pests. However, just by chance, a few insects may have genetic characteristics that confer resistance to the poison. The surviving individuals produce offspring, many of which inherit the resistance. As a result, a given concentration of the poison kills a smaller percentage of insects in the next generation; therefore, over time, the entire population may become highly resistant **(Figure 19.11).**

The Fossil Record. Because evolution results from the modification of existing species, Darwin's theory proposes that all species that have ever lived are genetically related. The fossil record documents such continuity, providing clear evidence of ongoing change in many **biological lineages**, evolutionary sequences of ancestral organisms and their descendants (see Chapter 22). For example, the evolution of modern birds can be traced from a dinosaur ancestor through fossils such as *Archaeopteryx lithographica* **(Figure 19.12).** This species, discovered only 2 years after *The Origin* was published, resembled both dinosaurs and birds. Like small carnivorous dinosaurs, *Archaeopteryx* walked on its hind legs and had teeth, claws on its forelimbs, and a long, bony tail. Like modern birds, it had hollow bones, an enlarged sternum, and feathers that covered its body.

Historical Biogeography. Analyses of **historical biogeography**, the study of the geographical distributions of plants and animals in relation to their evolutionary history, are generally consistent with Darwin's theory of evolution. Species on oceanic islands often closely resemble species on the nearest mainland, suggesting that the island and mainland species share a common ancestry. Moreover, species on a continental land mass are clearly related to one another and are often distinct from those on other continents. For example, monkeys in South America have long, prehensile tails and broad noses, traits that they inherited from a shared South American ancestor. By contrast, monkeys in Africa and Asia evolved from a different common ancestor in the Old World, and their shorter tails and narrower noses distinguish them from their American cousins.

Comparative Morphology. Other evidence of evolution comes from **comparative morphology**, analyses of the structure of living and extinct organisms. Such analyses are based on the comparison of **homologous traits**, characteristics that are similar in two species because they inherited the genetic basis of the trait from their common ancestor. For example, the forelimbs of all four-legged vertebrates are homologous because they evolved from a common ancestor with a forelimb composed of the same component parts (see Figure 19.3, which shows homologous bones in the same color). Even though the shapes of the bones are different in pigs, dolphins, and bats, similarities in the three limbs are apparent. The differences in structural details arose over evolutionary time, allowing pigs to walk, dolphins to swim, and bats to fly. The arms of humans and the wings of birds are also constructed of comparable elements, suggesting that they, too, share a common ancestor with the three species illustrated.

Comparative Embryology. The early embryos of different species within a major group of organisms are often strikingly similar. For example, certain components of the circulatory system emerge in all vertebrate embryos at corresponding stages of development **(Figure 19.13).** In addition, the early embryos of humans and other four-limbed vertebrates possess gill pouches (similar to those in adult fishes) and a tiny tail. These embryonic similarities indicate that fishes, amphibians, reptiles, birds, and mammals all evolved from a common ancestor. Additional genetic instructions have also evolved, causing their adult morphology to diverge.

Comparative Molecular Biology. The genes and proteins of different species also contain information about evolutionary relationships. The very existence of a common genetic code is powerful evidence for the relatedness of all forms of life. Moreover, some genes and their protein products are present in most living organisms, an observation that is most easily explained by the hypothesis of common ancestry. For example, cytochrome *c,* a protein involved in cellular respiration (see Section 8.4), is found within the mitochondria of all eukaryotic organisms. Evolutionary processes have modified the gene that codes for this protein, establishing variations in its amino acid sequence among different groups of organisms. Closely related species—for example, humans and their fellow primates, chimpanzees and rhesus monkeys—exhibit few differences in the amino acid sequence; more distantly related organisms, such as humans and yeast, exhibit many differences **(Figure 19.14).**

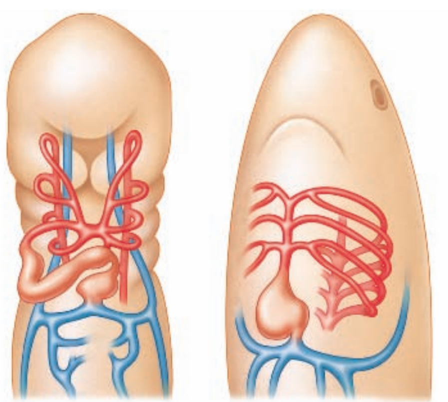


Figure 19.13
Embryologic clues to evolutionary history. Related species often show similar patterns of embryonic development. The aortic arches (red), a two-chambered heart (orange), and a set of veins (blue) in an early human embryo are also present in the embryos of other vertebrates. These structures persist into adulthood in some fishes, such as sharks.

Some People Misinterpret the Theory of Evolution

The theory of evolution has always been a contentious subject because it challenges deeply held traditional views of how living organisms originated. Many of Darwin's contemporaries were dismayed by the suggestion that all organisms share a common ancestry. Some people even misinterpreted this assertion as "humans evolved from chimpanzees or gorillas." But the theory of evolution makes no such claims. Instead, it suggests that humans and apes are descended from an apelike common ancestor (see Section 30.13). In other words, an ancient population of organisms left descendants, which now include the living species of apes, as well as our own species. Moreover, the theory recognizes that evolution is an ongoing process: humans and apes have been evolving up until this very moment and will continue to evolve for as long as their descendants persist.

Early in the twentieth century, some scientists embraced the notion of **orthogenesis,** or progressive, goal-oriented evolution. This idea, derived from the *Scala Naturae,* suggests that evolution produces new species with the goal of improvement "in mind." We now know that evolution proceeds as an ongoing process of dynamic adjustment, not toward any fixed goal. Natural selection preserves the genes of organisms that function well in particular environments, but it cannot predict future environmental change. Imagine a population of plants with genes that affect how well they function under wet versus dry conditions. After a 5-year drought, the population would include mostly dry-adapted plants. If a series of wet years follows the drought, these plants will be poorly adapted to the altered conditions. The process that favored drought-adapted plants operated under the prevailing dry conditions, not in anticipation of how conditions might change in the future.

Evolution is the core theory of modern biology because its explanatory power touches on every aspect of the living world. And the application of molecular techniques to the study of evolutionary biology has greatly enhanced our knowledge. Despite some common misunderstandings about what the theory predicts, the study of evolution is alive and

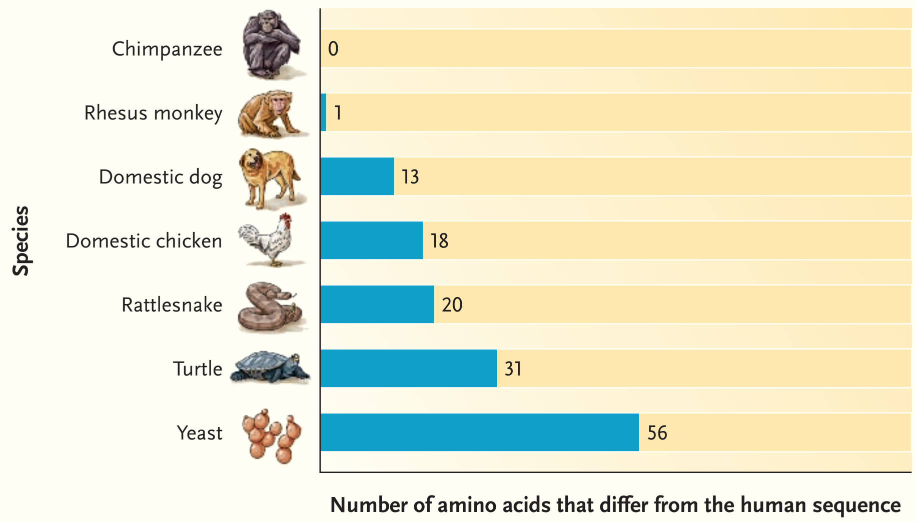
Figure 19.14 Observational Research

How Differences in Amino Acid Sequences among Species Reflect Their Evolutionary Relationships

HYPOTHESIS: The genetic instructions coding for proteins are more similar in closely related species than they are in more distantly related species.

PREDICTION: The amino acid sequences for a particular protein will be more similar in closely related species than in more distantly related species.

OBSERVATIONAL METHODS: Researchers gathered the amino acid sequences for the protein cytochrome *c* from a variety of organisms and compared them with the 104 amino acid sequence of this protein in humans.



RESULTS: Species that are closely related to humans, such as chimpanzees and rhesus monkeys, have amino acid sequences that are identical or nearly identical to the sequence in humans. More distantly related species, such as turtles and yeasts, exhibit sequences that are quite different from the sequence in humans.

CONCLUSION: Closely related species have very similar amino acid sequences in their proteins, reflecting similarities in their genetic makeup. More distantly related species exhibit substantial differences in amino acid sequences, reflecting the genetic divergence among them.

well. In fact, in late 2005, *Science* magazine, a prestigious scientific journal devoted to all of the natural sciences, declared "Evolution in Action" as the breakthrough of the year. The editorial staff cited exciting recent discoveries about genetic differences among organisms ranging from bacteria to humans, mechanisms that promote species formation, and the regulatory genes that may bridge the gap between microevolution and macroevolution.

In the remaining chapters of this unit you will discover how contemporary evolutionary theory explains changes at every level of biological organization from adaptive modifications within populations (see Chapter 20), to the development of new species (see Chapter 21), to the history of life (see Chapter 22), and the classification of all organisms on Earth (see Chapter 23).

Study Break

1. What two problems slowed the acceptance of Darwin's theory among scientists?
2. What is the difference between microevolution and macroevolution?
3. What types of data provide evidence that evolution has adapted organisms to their environments and promoted the diversification of species?

Unanswered Questions

What determines whether a species adapts to a changing environment or becomes extinct?

Natural selection has produced marvelous adaptations in every species on Earth, and we know that evolutionary adaptation to certain environmental changes has allowed many species to persist. But we also know that more than 99% of the species that have ever lived became extinct, evidently because they failed to adapt to changes in climate, natural competitors or enemies, or other environmental factors. But what kinds of genetic variation are required for adaptation, and what kinds of characteristics must evolve to allow survival? This is a critical question today, because human activities are changing environments so rapidly and drastically that many species face the threat of extinction. Can aquatic species adapt to various kinds of water pollution? Can animals and plants that lived in prairies adapt to different habitats, now that most prairies have been destroyed? Can Arctic species adapt to changes in climate as human production of carbon dioxide increases Earth's average temperature faster than ever before?

Is adaptation by natural selection responsible for most of the genetic differences between species?

New genetic variations sometimes become more common within populations or species because the proteins for which they code are advantageous and preserved by natural selection. But biologists who study molecular evolution have discovered that a large part of the genome in most organisms (about 98% of the human genome, for example) does not code for proteins and therefore appears to have no function. If this observation is generally correct, why do the noncoding parts of genomes exist? Are evolutionary changes in noncoding regions and the differences in noncoding sequences among species adaptive? For example, only about 1% of the DNA base pairs differ between human and chimpanzee genomes—but this amounts to about 34 million base-pair differences altogether, at least 60,000 of which alter the amino acid sequences of proteins. How can we determine which of these differences are adaptive and which differences underlie the unique characteristics of humans?

How do pathways of embryonic development evolve?

The characteristics of adult organisms are the product of developmental events, starting with the fertilized egg, that include growth in size, changes in the shape of various body parts, and the differentiation of cell types. These processes are largely controlled by genes, with input from the environment. Although biologists are beginning to learn how the genetic foundations of developmental processes evolve, many questions remain. For example, how do genetic changes induce differences in the branching patterns of antlers among species of deer, or differences in the length of the tails of monkeys and apes (including humans), or differences in the number and size of scales among species of lizards? We know that the proteins forming the lens of the eye are actually enzymes that play different roles in other cells, and that they have been "recruited" to form the lens, but what mechanisms induce them to assume this new role? And why do different enzymes form the lens in eyes of birds and mammals? Evolutionary developmental biology, which is discussed in Chapter 22, is one of the most active, exciting fields in biology at this time.

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Review

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19.1 Recognition of Evolutionary Change

- Ancient Greek philosophers classified the natural world, ranking inanimate objects and living organisms from simple to complex.
- Natural theologians, who merged Greek philosophy with the biblical account of creation, believed that all species were specially created and perfectly adapted. Existing species could not change or become extinct, and new species could not arise. Studies in biogeography, comparative morphology, and paleontology led scientists to wonder whether species might change through time (Figures 19.2 and 19.3).
- Lamarck developed the first comprehensive theory of biological evolution; he proposed that species evolved into more complex forms that functioned better in their environments. He hypothesized that structures in an organism changed when they were used, and that those changes were inherited by the organism's offspring. Experiments have refuted Lamarck's proposed mechanisms.
- Two geologists, Hutton and Lyell, recognized that major features on Earth were created by the long-term action of the very slow geological processes that scientists observe today. Their insights suggested that Earth was much older than natural theologians had supposed.

19.2 Darwin's Journeys

- Darwin's observations during his voyage on the *Beagle* provided much of the data and inspiration for the development of his theory of evolution (Figures 19.5–19.8).
- Darwin based the theory of evolution by means of natural selection on three inferences: (1) individuals within a population compete for limited resources, (2) hereditary characteristics allow some individuals to survive longer and reproduce more than others, and (3) a population's characteristics change over time as advantageous heritable characteristics become more common (Table 19.1).
- Darwin also proposed that the accumulation of differences fostered by natural selection could cause populations to diverge over time. Such evolutionary divergence can lead to the production of new species, which can, in turn, give rise to new evolutionary lineages (Figures 19.9 and 19.10).

Animation: The Galápagos

Animation: Finches of the Galpágos

19.3 Evolutionary Biology since Darwin

- Scientists working in population genetics developed theories of evolutionary change by integrating Darwin's ideas with Mendel's research on genetics.
- In the 1930s and 1940s, the modern synthesis provided a unified view of evolution that drew on studies from many biological disciplines. It emphasized evolution within populations, the central role of variation in the evolutionary process, and the gradualism of evolutionary change.
- Studies of adaptation, the fossil record, historical biogeography, comparative morphology, comparative embryology, and comparative molecular biology provide compelling evidence of evolutionary change (Figures 19.11–19.14).
- Evolutionary biology is an active field of study, and the application of molecular techniques is yielding new answers to old questions.

Questions

Self-Test Questions

1. Which of the following statements about evolutionary studies is *not* true?
   a. Biologists study the products of evolution to understand the processes causing it.
   b. Biologists design molecular experiments to examine evolutionary processes operating over short time periods.
   c. Biologists study the inheritance of characteristics that a parent acquired during its lifetime.
   d. Biologists study variation in homologous structures among related organisms.
   e. Biologists examine why a huge variety of species may inhabit a small island cluster.
2. Which of the following ideas is *not* included in Darwin's theory?
   a. All organisms that have ever existed arose through evolutionary modifications of ancestral species.
   b. The great variety of species alive today resulted from the diversification of ancestral species.
   c. Natural selection drives some evolutionary change.
   d. Natural selection preserves favorable traits.
   e. Natural selection eliminates adaptive traits.
3. The father of taxonomy is:
   a. Charles Darwin.
   b. Charles Lyell.
   c. Alfred Wallace.
   d. Carolus Linnaeus.
   e. Jean Baptiste de Lamarck.
4. The wings of birds, the legs of pigs, and the flippers of whales provide an example of:
   a. vestigial structures.
   b. homologous structures.
   c. acquired characteristics.
   d. artificial selection.
   e. uniformitarianism.
5. Which of the following statements is *not* compatible with Darwin's theory?
   a. All organisms have arisen by descent with modification.
   b. Evolution has altered and diversified ancestral species.
   c. Evolution occurs in individuals rather than in groups.
   d. Natural selection eliminates unsuccessful variations.
   e. Evolution occurs because some individuals function better than others in a particular environment.
6. Which of the following does *not* contribute to the study of evolution?
   a. population genetics
   b. inheritance of acquired characteristics
   c. the fossil record
   d. DNA sequencing
   e. comparative morphology
7. Which of the following could be an example of microevolution?
   a. a slight change in a bird population's color due to a small genetic change in the population
   b. large differences between fossils found near the ground surface and those found in deep rock layers
   c. the sudden disappearance of an entire genus
   d. the direct evolutionary link between living primates and humans
   e. a flood that drowns all members of a population
8. Which of the following ideas proposed by Lamarck was *not* included in Darwin's theory?
   a. Organisms change in response to their environments.
   b. Changes that an organism acquires during its lifetime are passed to its offspring.
   c. All species change with time.
   d. Genetic changes may be passed from one generation to the next.
   e. Specific mechanisms cause evolutionary change.
9. Medical advances now allow many people who suffer from genetic diseases to survive and reproduce. These advances:
   a. refute Darwin's theory.
   b. support Lamarck's theory.
   c. disprove descent with modification.
   d. reduce the effects of natural selection.
   e. eliminate adaptive traits.
10. The belief that evolution is progressive or goal-oriented is called:
    a. gradualism.
    b. uniformitarianism.
    c. taxonomy.
    d. orthogenesis.
    e. the modern synthesis.

Questions for Discussion

1. Explain why the characteristics we see in living organisms adapt them to the environments in which their ancestors lived rather than to the environments in which they live today.
2. Imagine a population of mice that includes both brown and black individuals. They live in a habitat with brown soil, where predatory hawks can see black mice more easily than they can see brown ones. Design a study that would allow you to determine whether the brown mice are better adapted to this environment than black mice.
3. Find examples from popular publications or advertisements for consumer products that misrepresent the theory of biological evolution. Explain how the theory is misrepresented.

Experimental Analysis

Design an experiment to test Lamarck's hypothesis that characteristics acquired during an organism's lifetime are inherited by their offspring. (You may wish to review the components of a well-designed experiment in Chapter 1 before formulating your answer.) Can you think of examples of acquired characteristics that are *not* inherited by offspring?

Evolution Link

Identify three discoveries or inventions that have changed how humans are affected by natural selection. Describe in detail how each discovery influences survival or reproduction in our species.

How Would You Vote?

A large asteroid could obliterate civilization and much of Earth's biodiversity. Should nations around the world contribute to locating and tracking asteroids? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.